

REVIEW OF THE *CENTROPHORUS* SHARKS (ELASMOBRANCHII, SQUALIDAE) OF THE EASTERN ATLANTIC

by

Ramon MUNOZ-CHAPULI and Fernando RAMOS (1)

ABSTRACT. - Results on systematics of the genus *Centrophorus* from the eastern Atlantic are yielded from an extensive study on body and skull morphometrics, dermal denticles, vertebral cuttings and fin rays. Our conclusions pointed out the validity of the following species inhabiting the area : *C. squamosus*, *C. granulosus*, *C. lusitanicus* and *C. niaukang*. The latter is recorded for first time from the Atlantic, although it had appeared in several accounts either as *C. granulosus* or *C. lusitanicus*. We propose synonymizing of *Squalus uyato* Raf., 1810 with an undetermined species of the genus *Squalus*, while *Dalatias nocturnus* Raf., 1810 should be regarded as junior synonym of *C. granulosus*.

RÉSUMÉ. - Des résultats sur la systématique du genre *Centrophorus* de l'Atlantique orientale sont présentés à partir de l'étude extensive de la morphométrie corporelle et crânienne, du squelette dermique, du nombre de vertèbres et des rayons de nageoires. Nos conclusions montrent la validité des espèces suivantes habitant cette zone : *C. squamosus*, *C. granulosus*, *C. lusitanicus* and *C. niaukang*. Cette dernière est citée pour la première fois de l'Atlantique, bien qu'elle avait été citée à plusieurs reprises comme *C. granulosus* ou *C. lusitanicus*. On propose de mettre en synonymie *Squalus uyato* Raf., 1810 avec une espèce indéterminée du genre *Squalus*, tandis que *Dalatias nocturnus* Raf., 1810 peut être considérée comme un synonyme junior de *C. granulosus*.

Key-words : Squalidae, *Centrophorus*, AE, East Atlantic, Taxonomy.

Sharks of the genus *Centrophorus* inhabit tropical and temperate seas in middle and great depths. They grow to a medium size ; less than 100 cm TL in most of the species. The genus *Centrophorus* is among the more confounded elasmobranch taxa in the eastern Atlantic. Among the most recent literature can be quoted : Cadenat and Blache (1981), describe three species groups (*C. granulosus*, *C. uyato* and *C. lusitanicus*) plus *C. squamosus* and *Centrophorus* sp. ; Compagno (1984), lists seven nominal species from which four inhabit the Atlantic ocean (*C. squamosus*, *C. granulosus*, *C. uyato*, and *C. lusitanicus*) ; McEachran and Branstetter (1984) report between eight and eleven nominal species, and five in the Clofnam area (the same listed by Compagno plus *C. machiquensis*) ; Bass *et al.* (1986) regard *Squalus uyato* as a *nomen dubium*, and list six valid species in need of revision.

Five nominal species have been, accordingly, considered as probably valid by most of the authors, but sometimes there are not agreement in the literature on the diagnostic features of these species, causing that specimens bearing very different characteristics receive the same specific status. Furthermore, the validity of three of the five nominal species (*C. uyato*, *C. machiquensis* and *C. lusitanicus*) is to be proved as stated by most of the recent authors. These problems are firstly due to the lack of detailed original descriptions and type material, and secondly to important morphological changes occur at the time of sexual maturity in some species of *Centrophorus*. These changes affect teeth, dermal denticles, colour and body proportions, and can be in the origin of some taxonomical confusion.

(1) Department of Zoology, Faculty of Sciences, University of Malaga. 29071 Malaga, SPAIN.

Taxonomists recognize that the genus *Centrophorus* is in need of revision. The present paper is a contribution to this revision, and concern the *Centrophorus* species of the eastern Atlantic (Fig. 1). We have done extensive comparison of material regarding the modern taxonomic features used in elasmobranch systematics.

The genus *Centrophorus* was established by Muller and Henle (1837) in order to separate from the older genus *Squalus* those species with extended inner corner of pectoral fins and dissimilar teeth in the jaws (pointed, triangular in upper, and blade-like in lower jaws). Günther (1870) extended the diagnosis of this genus to include several squalid species. Garman (1906) stated that the species included by Günther appear to group in four different genera, *Centrophorus*, *Acanthidium* Lowe, 1839; *Scymnodon* and *Centroscymnus* Bocage and Capello, 1864. This author included in *Centrophorus* three species from the E-Atlantic, *C. granulosus* Bloch & Schneider, 1801, *C. uyato* Raf., 1810 and *C. lusitanicus* Bocage and Capello, 1864. Bigelow and Schroeder (1948, 1957) and Bigelow *et al.* (1953) reincluded *C. squamosus* (Bonn., 1788) in the genus *Centrophorus*, in which it had been placed by Muller and Henle (1841), who did not consider that the differences in pectoral shape were enough to justify the genus *Lepidorhinus* established by Bonaparte (1838) for *S. squamosus* Bonn. This suggestion was not followed by Garman (1913) who revived *Lepidorhinus* for some leaf-like scaled species. The fifth nominal species described in the eastern Atlantic was *C. machiguensis* Maul, 1955, from Madeira; its status will be dealt with in the discussion. In this paper, eastern Atlantic refers only to the Mediterranean Sea and the area comprised between the parallels 5°N and 38°N, that is the area where most of the previous *Centrophorus* records have occurred.

MATERIAL AND METHODS

Material studied :

C. squamosus : UMDZ 87061101, female, 1245 mm TL. Specimen captured off the Atlantic coasts of Morocco, at 500 m depth.

C. granulosus : UMDZ 83100501, male, 565 mm TL ; UMDZ 83101101, male 555 mm TL ; UMDZ 83101704, male, 442 mm TL ; UMDZ 84011801, male, 226 mm TL ; UMDZ 84011802, female, 420 mm TL ; UMDZ 84011803, male, 368 mm TL ; UMDZ 84011804, female, 400 mm TL ; UMDZ 85072302, male, 448 mm TL ; UMDZ 85100301, male, 868 mm TL ; UMDZ 85100302, female, 746 mm TL ; UMDZ 85100303, male, 887 mm TL ; UMDZ 85100304, female, 665 mm TL ; UMDZ 85100802, male, 549 mm TL ; UMDZ 86020702, male, 478 mm TL ; UMDZ 86020703, female, 463 mm TL ; MNHN 1905-568, male, 452 mm TL ; MNHN 1969-216, male, 340 mm TL ; MNHN 1969-264 male, 399 mm TL ; MNHN 1969-269, male, 494 mm TL ; MNHN 1978-49, female, 928 mm TL.

The specimens were captured off the coasts of the following areas : southeastern Spain, Morocco (north and western), Tunisia, Portugal, Canary Islands, Ghana and Liberia, between 100-540 m depth.

C. lusitanicus : UMDZ 83111603, male 775 mm TL ; UMDZ 85030403, male 779 mm TL ; UMDZ 87061118, female 900 mm TL ; UMDZ 87061119, male 790 mm TL ; UMDZ 87061120, male 800 mm TL ; UMDZ 87061121, male 740 mm TL ; UMDZ 87061122, male 784 mm TL ; UMDZ 87061123, male 740 mm TL ; UMDZ 87061124, female 880 mm TL ; MNHN 1969-225, male 402 mm TL ; MNHN 1969-276, female 519 mm TL.

Specimens proceeding from the following areas : Atlantic coasts of Morocco (below 35° N), Canary Islands, Ghana and Cameroun, between 370-610 m depth.

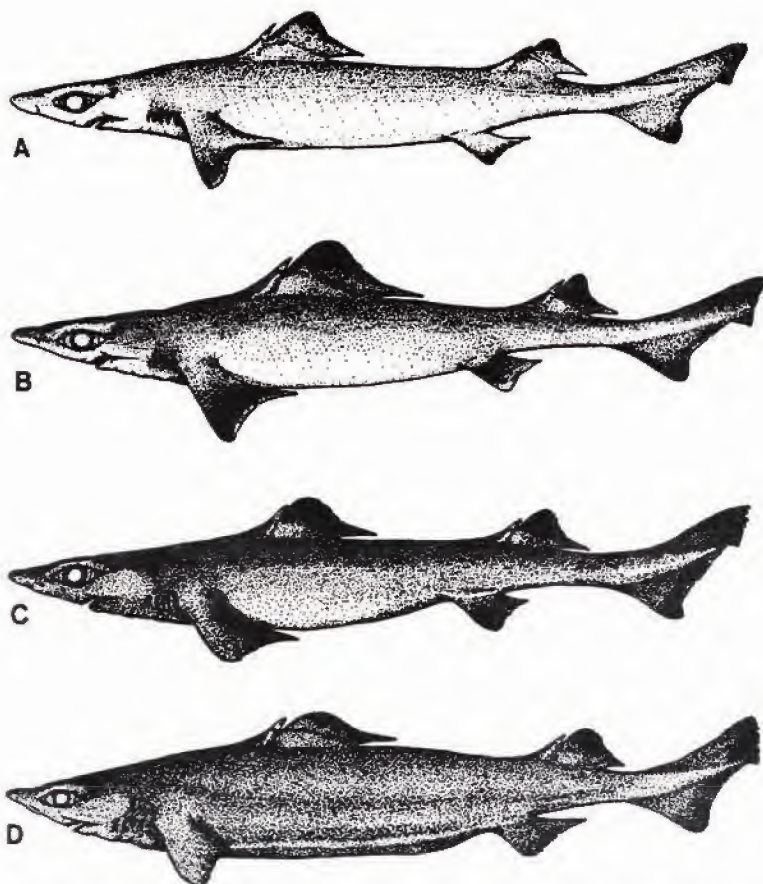


Fig. 1 : The *Centrophorus* species inhabiting the eastern Atlantic. Drawings from natural and photographs. A : *C. granulosus* ; B : *C. lusitanicus* ; C : *C. niaukang* ; D : *C. squamosus*.

C. niaukang : UMDZ 84122802, female, 614 mm TL ; UMDZ 85050601, male 875 mm TL ; UMDZ 85052101, female, 598 mm TL ; UMDZ 87061102, female, 745 mm TL ; UMDZ 87061103, female, 705 mm TL ; UMDZ 87061104, male 732 mm TL ; UMDZ 87061105, female, 658 mm TL ; UMDZ 87061106, female 676 mm TL ; UMDZ 87061107, female, 675 mm TL ; UMDZ 87061108, female, 630 mm TL ; UMDZ 87061109, female, 700 mm TL.

The specimens were captured in the Atlantic Ocean between 29° and 31° N, and in the between 470-720 m depth. All were immature.

Methods

Measurements of the specimens were done according to the criteria figured by Compagno (1984) and are expressed as a percentage of the total length.

The chondrocrania were obtained by cleaning in hot water. Chondrocranial measurements taken are shown in Figure 2. All are expressed as a percentage of the total length of chondrocranium (TLC). Vertebral numbers were established by dissection, boiling or from radiographs, according to the criteria of Springer and Garrick (1964). Skin samples for the observation of dermal denticles were obtained from the laterodorsal area, anterior to the first dorsal spine.

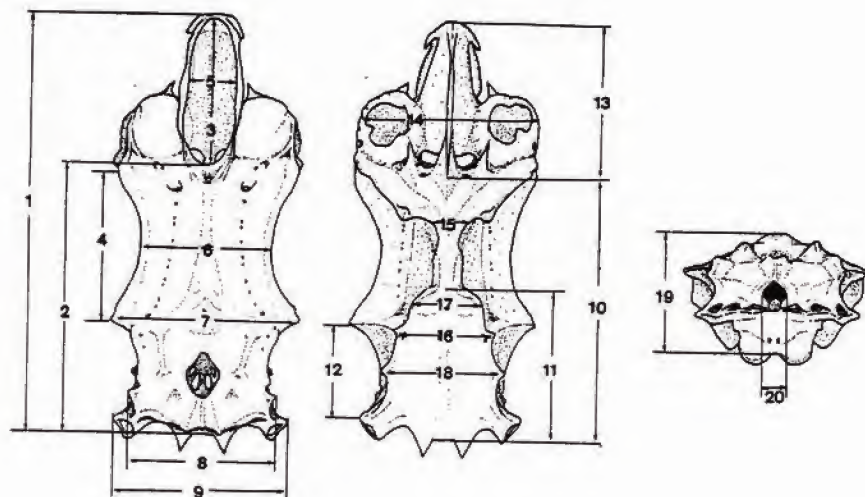


Fig. 2 : Chondrocranial measurements taken on the *Centrophorus* skull. Explanation of the measurements in Table III. A : dorsal view ; B : ventral view ; C : posterior view.

RESULTS

Body measurements

Table I shows body measurements of the study material excepting *C. squamosus*. Measurements of characters were compared between *C. granulosus*, *C. lusitanicus* and *C. niaukang* through an ANOVA test of differences between inter and intraspecific variances. Table II shows the significative morphometric differences at the 95 % or higher level of confidence. The main differences between *C. granulosus* and *C. lusitanicus* are in the following distances : snout tip-first dorsal origin, snout tip-first dorsal spine, first dorsal fin base (whether measured from the origin of the spine or from its anterior origin). Differences between *C. granulosus* and *C. niaukang* can be observed in the second dorsal fin base-caudal origin distance and in the length of the dorsal fin bases, measured from their anterior origin. *C. lusitanicus* and *C. niaukang* can be separated from the distances : tip snout-first dorsal fin origins, second dorsal fin base-caudal origin, and first dorsal fin base (whether measured from its anterior origin or from the origin of the spine).

Table I shows some key measurements taken on the possible syntype of *C. lusitanicus* (C.l.). These measurements agree very well with those from our *C. lusitanicus* specimens. Comparison between the body measurements of our *C. niaukang* specimens with those from the holotype (C.n. in Table I, taken from Teng, 1959) does not show any significant difference, except a shorter inner margin of pectoral fins in the latter (9,09 % TL against a mean value of 12,46% TL in our specimens). However, the figure of the holotype by Teng shows a damaged left pectoral fin, lacking of its inner corner. It could be the reason for the lower value, if it was obtained from the mean of both pectoral fins.

Table I : Number of specimens, mean values and standard deviation of the body measurements in three species of *Centrophorus*, and two type specimens. Explanation in the text.

	<u>C.granulosus</u>			<u>C.lusitanicus</u>			<u>C.nisakung</u>			<u>C.l. type</u>	<u>C.n.type</u>
Sex:	13 M - 6 F			3 M - 3 F			2 M - 9 F			M	F
Total length:	226-928 mm			402-900 mm			598-875 mm			742 mm	1540 mm
	N	\bar{x}	s	N	\bar{x}	s	N	\bar{x}	s		
Snout tip to:											
- Nostrils	19	3.53	.72	11	3.39	.45	11	4.29	.38	-	4.35
- Eye	19	6.17	.84	11	5.79	.38	11	6.65	.35	5.59	-
- Mouth	16	10.57	.70	11	9.38	.73	11	10.05	.78	-	8.44
- 1st gill	19	18.80	.92	11	17.03	1.01	11	18.96	.86	17.05	-
- Pectoral origin	16	23.00	2.01	11	20.66	1.44	11	22.14	1.04	-	23.36
- Anterior fold of first dorsal fin	18	32.02	1.09	11	25.40	.63	9	29.86	1.33	27.22	-
- 1st dorsal fin spine	5	36.37	.98	8	31.84	.61	10	35.77	.93	-	36.04
- 2nd dorsal fin spine	-	-	-	7	66.73	.76	8	67.37	1.12	-	-
- Anus	19	59.20	1.99	11	61.19	1.58	11	61.05	1.42	-	-
- Upper caudal origin	19	79.54	2.09	11	80.52	1.55	11	80.24	1.19	-	80.71
Distance between bases:											
- 1st and 2nd dorsal fins	5	24.18	2.68	7	23.78	.96	9	23.17	1.23	-	-
- 2nd dorsal and caudal fins	19	7.77	.74	11	7.89	.47	11	6.12	.49	8.02	4.22
- Pectoral and pelvic fins	19	30.42	2.47	11	33.69	2.97	11	31.40	1.32	-	-
- Pelvic and caudal fins	19	15.49	1.11	11	13.52	.96	11	13.19	.98	-	11.95
Nostrils:											
- Distance between inner corners	19	3.72	.39	11	3.30	.38	11	3.32	.42	-	3.18
- Distance between outer corners	19	6.90	.52	11	6.64	.35	11	6.85	.31	-	-
- Length	19	1.61	.21	11	1.82	.18	11	1.95	.18	-	-
Mouth:											
- Width	19	7.72	.81	11	6.90	.45	11	7.84	.36	-	7.60
- Length of preoral clefts	16	5.11	1.32	11	5.11	.56	11	6.12	.43	-	-
Eye:											
- Diameter	19/19	5.99	.61	11	5.90	.24	11	5.67	.43	-	3.31
Spiracles:											
- Distance between inner tips	19	7.02	.83	10	6.19	.51	11	6.99	.27	-	-
Gill openings:											
- Length of 1st	18	2.10	.30	10	1.99	.38	11	2.01	.33	-	2.60
- Length of 3rd	18	2.43	.26	11	2.46	.28	11	2.50	.29	-	2.99
- Length of 5th	18	3.11	.48	11	2.83	.22	11	3.21	.44	-	3.70
1st dorsal fin:											
- Base total length	18	11.41	1.10	11	18.10	.88	10	14.07	2.54	-	-
- Base length (from spine origin)	5	8.14	.42	8	11.19	.63	10	8.45	.29	-	8.51
- Height	19	6.05	.69	11	6.51	.57	11	5.39	.72	-	5.52
- Free posterior margin	19	6.22	.48	11	6.28	.58	11	6.60	.54	-	-
- Length of exposed spine	18	2.39	.46	11	2.03	.29	11	1.72	.42	-	-
2nd dorsal fin:											
- Base total length	19	7.74	1.14	11	9.65	.96	11	10.30	2.07	-	-
- Base length (from spine origin)	5	6.08	.20	8	6.01	.62	9	6.59	.39	-	7.01
- Height	19	4.60	.69	11	5.79	.33	11	5.03	.51	-	5.52
- Free posterior margin	19	4.50	.34	11	4.04	.55	11	4.70	.29	-	-
- Length of exposed spine	19	3.13	.57	11	2.29	.63	10	2.36	.59	-	-
Pectoral fins:											
- Base length	19	5.58	1.16	11	5.65	1.04	11	5.64	.71	-	-
- Length of anterior margin	19	11.70	.96	11	12.56	.52	11	11.87	.48	-	10.71
- Length of posterior margin	19	9.00	1.88	11	8.27	1.02	11	7.59	1.44	-	7.27
- Length of inner margin	19	12.24	1.75	11	12.39	.67	11	12.47	1.00	-	9.09
Pelvic fins:											
- Length of anterior margin	19	6.49	.63	11	7.39	.51	10	7.16	.85	-	-
- Overall length	19	10.37	.87	11	10.77	.37	11	9.45	.93	-	-
Caudal fin:											
- Length upper margin	18	20.15	1.67	11	18.19	1.67	10	19.56	.90	18.94	20.13
- Length lower anterior margin	19	11.91	1.26	11	12.54	.84	11	13.16	.71	-	12.79
Caudal peduncle:											
- Height	17	3.64	.28	11	3.75	.32	11	3.96	.24		

Chondrocranial measurements

Table III shows chondrocranial measurements taken on *C. granulatus*, *C. lusitanicus* and *C. niaukang* and the significant differences between these measurements through an ANOVA test. *C. lusitanicus* and *C. niaukang* measurements seem to be very similar, the main difference being a wider anterior part of the cranium (olfactive and ethmoidean regions) in the former (Figs 3B, C).

C. granulatus measurements are clearly different from those of the other species. It has a higher skull, with a wider precerebral fenestra, and larger interorbital and posterior tip-precerebral fenestra distances (Fig. 3A). *C. granulatus* and *C. lusitanicus* have particularly dissimilar chondrometric results, with 12 from 19 sample means significantly different through an ANOVA test (Table III).

Table II : Comparison of *C. granulatus* (C.g.), *C. lusitanicus* (C.l.) and *C. niaukang* (C.n.) through an ANOVA test. Explanation in the text. (\bar{x} = mean values, f = variance ratio, df = degrees of freedom, "-" = not significant, * = significant with $p > .95$, all the f values without * are significant with $p > .99$)

	\bar{x} C.g.	\bar{x} C.l.	\bar{x} C.n.	C.g./C.l. f df		C.g./C.n. f df		C.l./C.n. f df	
Snout tip to:									
- Nostrils	3.53	3.39	4.29	-		10.46	28	25.66	20
- Eye		5.79	6.85	-		-		30.48	20
- Mouth	10.57	9.38	10.06	18.20	25	-		4.46*	20
- 1st gill	18.80	17.03	18.96	24.03	28	-		23.28	20
- Pectoral origin	23.00	20.66	22.14	10.97	25	-		7.64	20
- Ant. fold 1st dorsal fin	32.02	25.40	29.86	334.29	27	20.37	25	97.81	18
- 1st dorsal fin spine	36.37	31.84	35.77	107.74	11	-		105.72	16
- Anus	59.20	61.19	61.05	8.03	28	7.30*	28	-	
Distance between bases:									
- 2nd dorsal and caudal fins	7.77	7.89	8.12	-		43.32	28	74.75	20
- Pectoral and pelvic fins	30.42	33.69	31.40	10.53	28	-		5.46*	20
- Pelvic and caudal fins	15.49	13.52	13.19	24.11	28	32.47	28	-	
Nostrils:									
- Dist. between inner corners	3.72	3.30	3.32	8.23	28	6.93*	28	-	
Mouth:									
- Width	7.72	6.90	7.84	9.48	28	-		29.27	20
- Length of preoral clefts	5.11	5.11	6.12	-		5.94*	25	22.51	20
Spiracles:									
- Dist. between inner tips	7.07	6.19	6.99	9.29	27	-		20.75	18
Gill openings:									
- Length of 5th		2.83	3.21	-		-		6.56*	20
1st dorsal fin:									
- Base total length	11.41	18.10	14.07	291.39	27	15.04	26	24.56	19
- Base length (from spine)	8.14	11.19	8.45	90.37	11	-		151.02	16
- Height	8.05	6.51	5.39	-		6.18*	28	16.36	20
- Length exposed spine	2.39		1.72	-		15.44	27	-	
2nd dorsal fin:									
- Base total length	7.74	9.65	10.30	21.82	28	19.30	28	-	
- Base length (from spine)	6.08	6.01	6.59	-		7.25*	12	5.47*	15
- Height	4.60	5.79	5.03	28.60	28	-		17.22	20
- Free posterior margin		4.04	4.70	-		-		12.39	20
- Length exposed spine	3.13	2.29	2.36	14.02	28	11.68	27	-	
Pectoral fins:									
- Length anterior margin	11.70	12.56	11.87	7.48*	28	-		10.46	20
- Length posterior margin	9.00		7.59	-		4.60*		-	
Pelvic fins:									
- Length anterior margin	6.49	7.39	7.16	16.21	28	5.82*	27	-	
- Overall length	10.37	10.77	9.45	-		7.41*	28	19.13	20
Caudal fin:									
- Length upper margin	20.15	18.19	19.56	9.40	27	-		5.31*	19
- Length lower ant. margin	11.91		13.16	-		9.07	28	-	
Caudal peduncle:									
- Height	3.64		3.96	-		9.71	28	-	

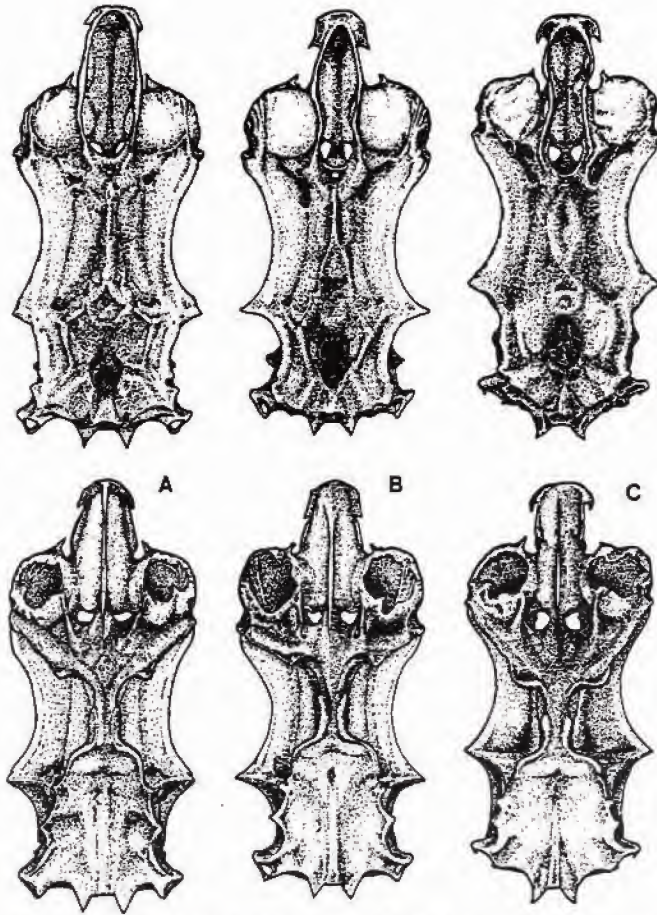


Fig. 3 : Dorsal (above) and ventral (below) views of the chondrocrania of three species of *Centrophorus*. Drawings from natural. A : *C. granulosus* ; B : *C. lusitanicus* ; C : *C. niaukang*.

Dermal denticles

As it has been reported by several authors, dermal denticles of *C. squamosus* are large (about 1.7 mm wide) with leaf-like crown (Fig. 4A), strong median cusp and 3 or more lateral cusplets.

C. niaukang dermal denticles are clearly different from the other species, sessile, almond-shaped, with one acute posterior cusp, about 0.5-1 mm wide. A single or double main keel runs along most of the scute surface, and there are 1-2 secondary keels on each side, mainly in the larger denticles (Fig. 4E). *C. granulosus* and *C. lusitanicus* share very similar dermal denticles, small and pointed in the young and large, block-like, sessile-crowned, regularly arranged dermal denticles on the sides of adults (Figs 4B, C, D).

Differences between dermal denticles of these species were widely discussed by Cadenat (1959) and Cadenat and Blache (1981), although there were in their descriptions some cases of misidentification, as it will be discussed below. Compagno's (1981 and 1984) figures of *C. lusitanicus* dermal denticles, taken from Bass *et al.* (1976) agree with our description of *C. niaukang* denticles. On the other hand, differences between young and adult specimens of *C. granulosus* are among the causes of the taxonomic problems raised by *C. uyato*. These problems will be dealt with below.

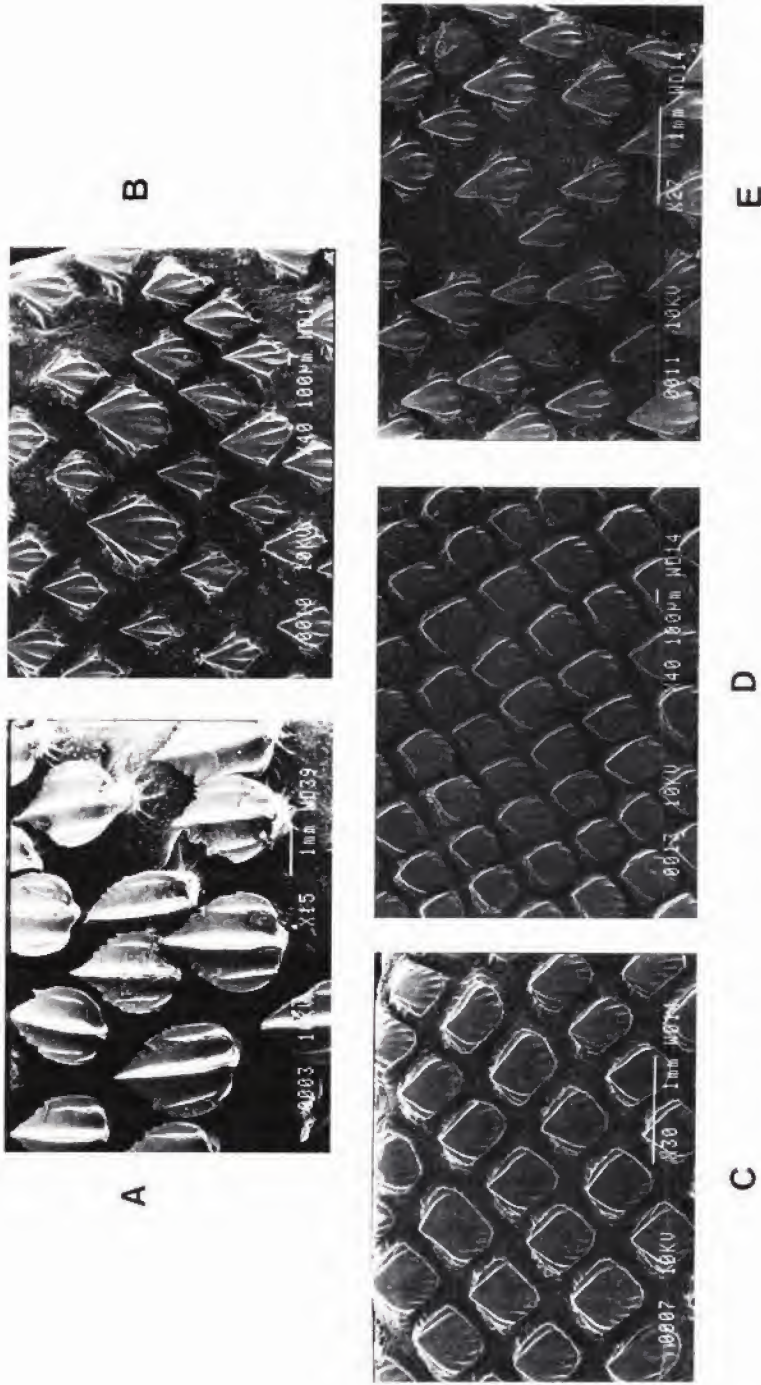


Fig. 4 : Dermal denticles of the studied *Centrophorus* species, photographed by scanning electron microscopy. A : *C. squamosus*, female, 1245 mm TL ; B : *C. granulosus*, young male, 555 mm TL ; C : *C. granulosus*, adult male, 887 mm TL ; D : *C. lusitanicus*, adult male, 779 mm TL ; E : *C. niaukang*, young female, 598 mm TL.

Teeth

Teeth were observed from several specimens of *C. granulosus*, *C. lusitanicus* and *C. niaukang*. It was observed a large variability among young and adults, mainly in the serration of lower and inclination of upper central teeth cusps, more remarkable in young specimens. Detailed description of teeth needs further attention, because of the differences due to sex, age, and position in the jaw, which can shade the interspecific differences. It will be dealt with in a separate paper.

Number of vertebrae

Monospondylous and precaudal vertebral numbers of the studied specimens are shown in Table IV, together with countings taken from the literature.

C. lusitanicus and *C. niaukang* showed a similar number of vertebrae, slightly higher than that of *C. granulosus*. The species called "*C. lusitanicus*" by Bass *et al.* (1976) in western South Africa (probably *C. niaukang*, see below) showed a lesser vertebral counting than the *C. niaukang* from north eastern Atlantic (80-83 instead of 86-90 precaudal centra from our specimens). This is the main difference between these two forms. The species called by the same authors "*C. uyato*" agrees well in vertebral countings with our *C. granulosus*, as does the single counting of "*C. uyato*" from E-Atlantic reported by Springer and Garrick (1964). The possible syntype of *C. lusitanicus* has 59 monospondylous, 88 precaudal and 121 total vertebral centra, a number very similar to that obtained from our *C. lusitanicus* specimens.

Number of rays in dorsal fins

The number of rays, counted in the middle series (Fig. 5), from the four studied *Centrophorus* species, is given in Table V. *C. lusitanicus* showed a larger number of rays in both dorsal fins than the remaining studied species, specially in the first one. The observed range for this fin (16-19 rays counted in the middle series, Fig. 5C), doubles the countings for *C. granulosus* and *C. niaukang*. The only dissected specimen of *C. squamosus* had 13 rays in the first dorsal fin, intermediate between its congeneric species.

Number of rays in pectoral and pelvic fins

The results of the pectoral and pelvic rays counting are given in Table V. Both were counted in the middle series, as shown by Figures 6 and 7. *C. lusitanicus* seems to have a slightly larger number of rays in pectoral fins (22-27), while the single studied *C. squamosus* specimen had 19. However, conspicuous differences in the number of pelvic fin rays were not observed (Fig. 7).

DISCUSSION

From the results it can be concluded that at least four species of the genus *Centrophorus* inhabit the E-Atlantic ocean (Fig. 1). Their diagnostic features, and the names that should be assigned to them, are as follows:

C. squamosus: the angular, not produced inner corner of the pectoral fins and the large, leaf-like dermal denticles, allow easy discrimination between this species and its congeners.

C. granulosus: inner pectoral margin very produced, first dorsal fin short and high, with base (measured from the origin of the fold) less than 14% of TL, dermal denticles small and pointed in the young. They are sessile-crowned, block-like, blunt, regularly arranged in adult specimens.

Table III : Number of measured chondrocrania, mean values and standard deviation. Comparison between measurements of the three species, through an ANOVA test, is shown. (\bar{x} = mean values, f = variance ratio, df = degrees of freedom, "-" = not significant, * = significant with $p > .95$, all the f values without * are significant with $p > .99$. The numbers of the measurements correspond with those on figure 2).

1. Total length of the chondrocranium	C. granulosus			C. lusitanicus			C. niangkang			C.g./C.l.		C.g./C.n.		C.l./C.n.	
	N	\bar{x}	s	N	\bar{x}	s	N	\bar{x}	s	$\frac{f}{f}$	$\frac{d.f.}{d.f.}$	$\frac{f}{f}$	$\frac{d.f.}{d.f.}$	$\frac{f}{f}$	$\frac{d.f.}{d.f.}$
2. Posterior tip-precerebral fenestra	18	65.76	2.73	7	61.97	2.33	4	60.29	.82	10.34	23	15.24	20	-	-
3. Length precerebral fenestra	18	35.17	3.02	7	38.11	2.32	4	39.38	.85	5.35*	23	7.36*	20	-	-
4. Distance between orbital processes	18	37.83	3.42	7	34.97	1.73	4	35.40	1.39	4.38*	23	-	-	-	-
5. Precerebral fenestra width	18	12.19	2.13	7	9.28	.97	4	7.70	.55	11.89	23	16.92	20	8.77*	9
6. Interorbital width	18	33.31	1.46	7	30.53	1.76	4	30.20	1.05	16.34	23	15.99	20	-	-
7. Postorbital width	18	47.97	3.06	7	45.88	2.09	4	45.60	1.12	-	-	-	-	-	-
8. Distance between pterotic processes	18	35.68	3.20	7	30.85	2.28	4	32.87	.82	13.19	23	-	-	-	-
9. Distance between hyomandibular facets	18	42.63	3.32	7	40.55	1.09	4	40.89	.93	-	-	-	-	-	-
10. Posterior tip-rostral keel origin	18	62.64	4.31	7	55.77	5.62	4	59.88	1.69	9.44	23	-	-	-	-
11. Posterior tip-basal-angle	18	38.24	2.64	7	38.04	1.37	4	35.41	1.34	-	-	-	-	9.58*	9
12. Postorbital process-hyomandibular facet	18	23.81	1.61	7	21.38	2.44	4	21.52	1.41	8.60	23	-	-	6.85*	20
13. Length of rostral keel	18	41.14	4.51	7	43.03	9.13	4	42.39	2.35	-	-	-	-	-	-
14. Width across nasal capsule	17	43.28	1.44	7	45.21	1.30	4	41.72	2.59	-	-	9.58	22	-	-
15. Subethmoidal width	18	8.35	1.48	7	10.12	1.83	4	6.55	.34	6.30*	23	5.65*	20	14.33	9
16. Width of anterior basal plate	18	27.11	1.91	7	25.48	2.41	4	28.19	1.20	-	-	-	-	-	-
17. Width of basal angle	18	19.48	2.26	7	22.07	1.65	4	21.58	.62	7.56*	-	-	-	-	-
18. Width of posterior basal plate	18	32.83	1.81	7	30.87	4.02	4	32.35	1.10	-	-	-	-	-	-
19. Maximum sagittal height	18	26.97	1.91	7	25.20	1.48	4	24.96	.62	21.88	23	16.65	20	-	-
20 Width of foramen magnum	18	5.79	.96	7	5.45	.67	4	5.30	1.02	-	-	-	-	-	-

Table IV : Vertebral counts in *Centrophorus*. * Range and mean value of "*C. uyato*" (= *C. granulosus*) after Bass *et al.* (1976) and Springer and Garrick (1964). ** Range and mean value of "*C. lusitanicus*" (= *C. niangkang*) after Bass *et al.* (1976).

	NONSpondyLOUS CENTRA												PRECAUDAL CENTRA											
	53	54	55	56	57	58	59	60	61	64	79	80	81	82	83	84	85	86	87	88	89	90	91	92
<i>C. squasosus</i>																								
<i>C. granulosus</i>	1	2	1	4	2						1					1		2	2	2				
" <i>C. uyato</i> "**																								
<i>C. lusitanicus</i>											1	1	1								2	1	1	
<i>C. lusitanicus</i> (type)											1										1			
" <i>C. lusitanicus</i> "**																								
<i>C. niangkang</i>	1		1	1	1																3		1	

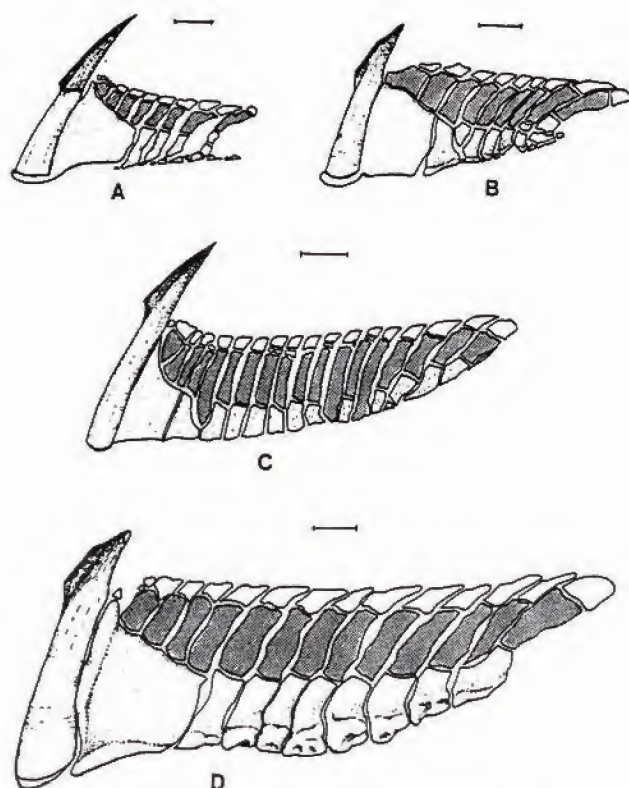


Fig. 5 : First dorsal fin skeleton in the studied *Centrophorus* species. Middle series of rays is shown by the plot. A : *C. granulosus*, male, 746 mm TL ; B : *C. niaukang* female, 630 mm TL ; C : *C. lusitanicus*, male, 790 mm TL ; D : *C. squamosus*, female, 1245 mm TL. (Scale bar = 100 mm).

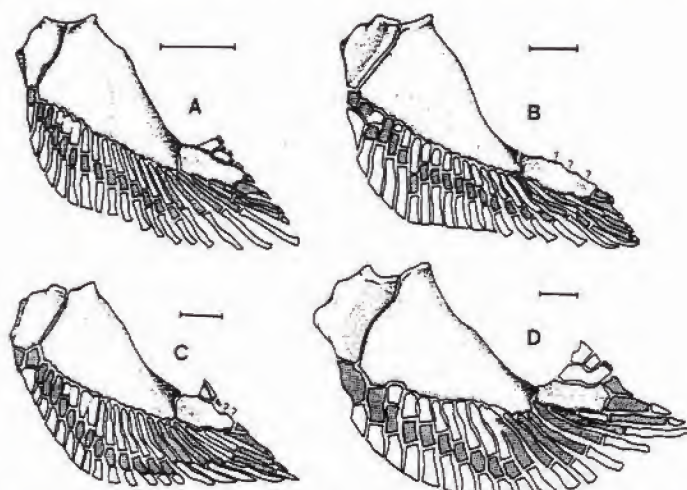


Fig. 6 : Pectoral skeleton in the studied *Centrophorus* species. Middle series of rays is shown by the plot. A : *C. granulosus*, male, 442 mm TL ; B : *C. lusitanicus*, male, 715 mm TL ; C : *C. niaukang*, female, 630 mm TL ; D : *C. squamosus*, female, 1245 mm TL. (Scale bar = 100 mm).

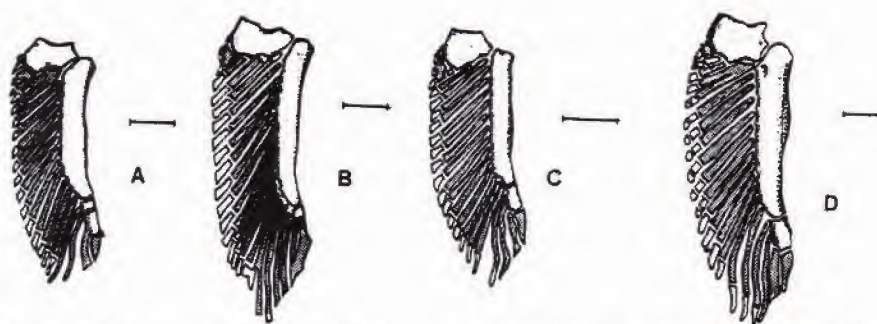


Fig. 7 : Pelvic skeleton in the studied *Centrophorus* species. A : *C. granulosus*, female, 746 mm TL ; B : *C. lusitanicus*, female, 880 mm TL ; C : *C. niaukang*, female, 676 mm TL ; D : *C. squamosus*, female, 1245 mm TL (Scale bar = 100 mm).

Table V : Fin ray counts in *Centrophorus*.

NUMBER OF RAYS:	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
<i>C. squamosus</i>										1															1st dorsal Fin
<i>C. granulosus</i>					1	2	2																		
<i>C. lusitanicus</i>													1	1	1	1									
<i>C. niaukang</i>					1		3																		
<i>C. squamosus</i>					1																				2nd dorsal Fin
<i>C. granulosus</i>				3	1	1																			
<i>C. lusitanicus</i>					2	2																			
<i>C. niaukang</i>				1	1	2																			
<i>C. squamosus</i>																1									Pectoral Fin
<i>C. granulosus</i>																	6	3	2						
<i>C. lusitanicus</i>																		1	2		1		1		
<i>C. niaukang</i>																				3	1				
<i>C. squamosus</i>																					1				Pelvic Fin
<i>C. granulosus</i>																		1	1	3	3	2			
<i>C. lusitanicus</i>																		1	1	1	1	1			
<i>C. niaukang</i>																				3	1				
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	

C. lusitanicus : inner pectoral fin margin and dermal denticles like in young and adult specimens of *C. granulosus*, but the first dorsal fin is longer, with base (measured from the origin of the fold) larger than 16% of TL. The snout tip-first dorsal fin origin is about 25% TL (30%-32% TL in *C. niaukang* and *C. granulosus*), while the snout tip-first dorsal spine distance is about 32% TL (36% in the other two species).

C. niaukang : inner pectoral fin margin as long as in the other species but not produced. Colour very dark, with white dots because of the decalcified denticles. First dorsal fin length of intermediate size between those of *C. granulosus* and *C. lusitanicus*. Second dorsal fin base-caudal origin distance (about 6 % of total length about 7.5-8% TL in *C. granulosus* and *C. lusitanicus*). Dermal denticles large and very pointed, almond-shaped, with strong ridges. Adults longer than 90-100 cm, (75 and 82 cm in *C. lusitanicus* and *C. granulosus*, respectively).

We will justify now our decision concerning the nominal species to which they were assigned, and we will discuss some nomenclatural questions.

First of all, we will deal with the validity of *C. uyato*. Authors who considered this nominal species as valid, with more or less doubts, were : Günther (1870), Garman (1913), Fowler (1936), Poll (1951), Dieuzeide *et al.* (1953), Bigelow, Schroeder and Springer (1953), Bigelow and Schroeder (1955, 1957), Tortonese (1956), Bini (1967), Sara (1968), Blache *et al.* (1970), Krefft and Tortonese (1973), Bass *et al.* (1976), Cadenat and Blache (1981) and Compagno (1981, 1984), among others. Authors who regarded *C. uyato* as invalid and based on young specimens of *C. granulosus*, are : Lozano Rey (1928), Maurin (1968), Maurin and Bonnet (1970), Quignard and Capapé (1971) and Munoz-Chapuli (1982). A third alternative was to include the original description of *Squalus uyato* by Rafinesque (1810) in the synonymy of an indetermined *Squalus* species. That was proposed by Regan (1908) and refuted by Garman (1913). Notwithstanding this opinion will be held in this account. Recently, Bass *et al.* (1986) have considered *S. uyato* as *nomen dubium*.

Actually, most of the authors who described *C. uyato* used features characteristic of young specimens of *C. granulosus* (pointed dermal denticles, upper teeth cusps more bent, lower teeth cusps serrated, etc.). However, an exhaustive review of the original description of *Squalus uyato* does not leave room for doubt, because of the following reasons :

1. Rafinesque did not mention any feature that relates his *Squalus uyato* with the genus *Centrophorus*, with the exception, perhaps, of the "sharp" teeth, which hardly could be interpreted as "upper teeth triangular".

2. Some features of *Squalus uyato* fit well with those of some species of the genus *Squalus*, for example "color and size as *Galeus mustelus* (= *M. mustelus*)" or "a third of the length of the dorsal spine joined to the dorsal fins".

3. The figure of *S. uyato* of the original description (pl. XIV, fig. 2) does not fit with any *Centrophorus* species, but some details of the drawing (for example the caudal fin shape without apical lobe) suggest a *Squalus* species.

4. The name "ujatu" or "ujato" given by Rafinesque to this species is similar to the common name given to *Squalus acanthias* by the same author ("ujatu impiriali").

5. The species of the genus *Squalus* were known by the fishermen, in some areas of the western Mediterranean, as "Agullats" or "Ahullats" ("Aiguillats" in French), from where derived the common name "uyat" or uyato" (Buen, 1926). However, the species of the genus *Centrophorus*, at least in the Spanish coasts, are known as "quelvachos" or "guchos" (Lozano, 1963).

6. Probably, the most significative reason to remove *Squalus uyato* from the genus *Centrophorus* is that this genus *Centrophorus* is actually present in the paper by Rafinesque under another nominal species, very often neglected by the taxonomists. This species is *Dalatias nocturnus*, whose description agrees very well with some *Centrophorus* species. For example, the description includes the following statements : "The total length seldom reaches three feet and the teeth are dissimilar ... a half of the length of the dorsal spines joined to the dorsal fins ... beautiful skin, with many little tubercles closely set, but separate, smooth, rounded, with slightly striated margin ⁽¹⁾."

(1) "...rare volte giunge alla lunghezza di tre piedi : hi a i denti iniguali...la spina delle ali dorsali e unita all'ale nella meta de sua lunghezza...la sua pelle e bellissima e viene composta d'una moltitudine di tubercolletti situati l'uno vicino all'altro, sebbene ognuno sia distinto, piatto, rotondo, col margine leggermente striato".

Furthermore, the drawing of *Dalatias nocturnus* by Rafinesque (pl. XIV, fig. 3) shows a very produced inner margin in the pectoral fin, like in some *Centrophorus* species.

The exposed reasons strongly suggest that *S. uyato* should be regarded as synonym of an indeterminate species of the genus *Squalus*, maybe *S. blainvillei* or, most probably because of its abundance in the Mediterranean (Munoz-Chapuli and Ramos, in press), *S. megalops*. On the other hand, *Dalatias nocturnus* should be considered as synonym of a species belonging to the genus *Centrophorus*, most probably of *C. granulosus* the only species of this genus recorded in the Mediterranean.

This decision should not have any incidence on the status of the genus *Dalatias* Rafinesque, 1810 (older than *Centrophorus* Muller & Henle, 1837), since the type species of *Dalatias*, by subsequent designation by Jordan *et al.* (1913), is *Dalatias sparophagus* (= *Dalatias licha*), as has been accepted by most of the recent authors (Bigelow and Schroeder, 1948 ; Garrick, 1960 ; Bass *et al.* 1976 ; Compagno, 1984). However, most of the older authors stated that there are no grounds to synonymize *D. sparophagus* with *Squalus licha* Bonnaterre, 1788, since the former is a *species dubium*. If the designation of *D. sparophagus* as type species were invalidated by a ruling from the International Commission of Zoological Nomenclature, *Dalatias* would become an older synonym of *Centrophorus*, with important consequences for the nomenclatural stability.

The second taxonomic problem is that of *C. lusitanicus*, described by Bocage and Capello (1864), but refuted by the same authors two years later (Bocage and Capello, 1866). Lozano Rey (1928), Maurin (1968), Maurin and Bonnet (1970), and Quignard and Capapé (1971) considered this species as not valid. Günther (1870), Regan (1908), Garman (1913), Nobre (1935), Bigelow and Schroeder (1957), Cadenat (1959) and Blache *et al.* (1970) and Cadenat and Blache (1981) included this species in their accounts. Finally, Bass *et al.* (1976) and Compagno (1981, 1984) considered it as valid, but their descriptions agree better with *C. niaukang*, as it will be commented below.

As showed by the results, the specimens called by us *C. lusitanicus* belong to a definite species, different from the rest of E-Atlantic *Centrophorus*. The possible type specimen of *C. lusitanicus* (BMNH 1867.7. 23.2.) agrees with our specimens in measurements, number of vertebrae, pectoral fin shape and dermal denticles. It dissipates some doubts raised by two statements in the original description by Bocage and Capello (1864) : "black-violaceous colour" and "larger size than *C. granulosus*", that might suggest some relation with *C. niaukang*.

The distribution of *C. lusitanicus* includes the type locality (off Portugal) and the tropical and subtropical eastern Atlantic. There are not known records of this species from the Mediterranean or other oceans.

C. niaukang is a species described by Teng (1959) off Taiwan, of which exists very little information. Our specimens agree with the original description of the holotype in measurements, dermal denticles, colour, pectoral shape, and size (larger than other species of the genus). The recognition of *C. niaukang* in the eastern Atlantic is the key to resolve some of the taxonomic confusion surrounding the genus *Centrophorus* in the literature. This species was recorded as *C. lusitanicus* off Natal and Mozambique channel by Bass *et al.* (1976). For this reason it was also included under this specific name in the accounts by Compagno (1981, 1984). However, Cadenat and Blache (1981) rightly identified *C. lusitanicus*, but they reported the specimens of *C. niaukang* under the name *C. granulosus*, while the true *C. granulosus* appeared as "*C. uyato-machiquensis*".

The known distribution of *C. niaukang* includes the type locality (China Sea), southwestern Indian ocean and the tropical and subtropical eastern Atlantic. At present, there are not known records of this species from the Mediterranean.

Other nominal species, provisionally considered in this account as not-valid, is *C. machiquensis*, described off Madeira. Although we were unable to study the type material, there is nothing in the original description by Maul (1955) that allows differentiation between *C. machiquensis* and *C. granulosus*. Furthermore, Cadenat and Blache (1981), after an examination of the type specimen, concluded that *C. machiquensis* is conspecific with the specimens called by them *C. uyato*. Both were grouped in the "form *C. uyato-machiquensis*" by these authors. Since the specimens called *C. uyato* by them clearly agree with our *C. granulosus*, the statements by Cadenat and Blache support our proposal of synonymizing *C. machiquensis* and *C. granulosus* while new studies on the Madeira *Centrophorus* populations are carried out.

Some questions remain open at present, but it might be impossible to answer them. For instance, which *Squalus* species is the senior synonym of *S. uyato*? If it was *S. megalops*, this nominal species would become junior synonym of *S. uyato*. Which species was described by Bloch and Schneider (1801) as *C. granulosus*? Their reference to a five-foot specimen suggests that it could have been *C. niaukang*.

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